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Research paper

Hydrodynamic constraints on the evolution and ecology of planktic foraminifera☆

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ABSTRACT

The origin and function of a biomineralised skeleton in many of the non-motile groups of plankton remains an open question. Morphological diversity within these groups has often been explained by its relevance to hydrodynamic behaviour, principally buoyancy and settling. Consequently, ecological and evolutionary patterns of morphology have been associated with changes in surface water properties, but these hypotheses have rarely been critically assessed. Computational Fluid Dynamics simulations present a way to quantify the relative effect of size (maximum diameter), shape of the test and density (ratio between calcite and cavity volumes) of the specimen on settling velocity, as all variables can be manipulated independently. Here we interrogate the morphological diversity in planktic foraminifera as model organisms to explore the range of evolutionary options open to plankton to modulate settling velocity under varying environmental conditions. The evolutionary changes in morphology required to accommodate physical changes in the upper water column due to environmental changes, such as increased temperature, are small compared to the ecophenotypic variability of the population. In the modern ocean, the pattern of species distribution with depth is not likely to be determined by hydrodynamics as it is inconsistent with predictions based on settling velocity. These results suggest that intrinsic constraints on size, shape and calcification, such as heritage, exposure of the symbionts to light or oxygen diffusion into the cell, are likely to be more important than hydrodynamic function in determining the depth distribution and test morphology of planktic foraminifera.

1. Introduction

Gross adult morphology is a compromise between function and constraints arising from genetic heritage, development and energetic and constructional costs, modulated by the way the environment acts upon them. The origin and function of a biomineralised skeleton in many of the non-motile groups of plankton remains an open question; the perceived benefits of cellular support and protection from the biological, physical and chemical stresses of the ocean (Armstrong and Brasier, 2005) are offset by the negative buoyancy conferred by the skeleton to the organisms. A shell causes them to sink through the water column, potentially limiting their residence time in the specific layers of the ocean where the conditions for their optimal growth prevail.

The high morphological diversity and multi-species co-existence observed in plankton groups in an apparently uniform environment (Hutchinson, 1961; Shoresh et al., 2008) have in part been attributed to a successful exploitation of vertical resource heterogeneities (Roy and Chattopadhyay, 2007). It has been suggested that increasing density is in fact one of the adaptive roles of the skeleton as an integral part of a mechanism to regulate buoyancy and water column occupation of the organisms (Marszalek, 1982; Raven and Waite, 2004). The sinking effect, though, must still be counteracted or controlled in order for the organism to remain at, or migrate into, the appropriate depths. Both extrinsic and intrinsic mechanisms to compensate for the negative buoyancy of the skeleton have been put forward (Reynolds, 2006). These mechanisms include relying on the physical mixing of the surface layers of the ocean for turbulent resuspension (Huisman et al., 2002), the physiological regulation of the cytoplasmic composition through incorporation of gas vesicles or changes to ionic concentration to reduce the overall density of the organism (Kahn and Swift, 1978; Walsby et al., 1997), and the use of morphological features of the skeletons themselves, including their size, general shape, and drag-inducing ornamentation (Smayda, 1970).

An ideal group to investigate the importance of morphological changes on water column position and hence vertical habitat separation are planktic foraminifera. Due to the low organisational level and small size of planktic foraminifera, the adaptive significance of the various test forms has been considered uncertain (Cifelli, 1969; Bonner, 2013). A possible functional control on morphology in this group, however, has been suggested based on the repeated evolution of a limited and stereotyped suite of morphological designs and features following extinction events: spherical and globular forms composed of near-spherical

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chambers, and flattened discoidal and conical tests made up of wedge-shaped chambers developing an outer keel (Cifelli, 1969; Norris, 1991a, 1991b).

A close relationship between morphology in planktic foraminifera and environmental parameters has been demonstrated repeatedly both in the fossil record and the modern ocean (Hecht and Savin, 1972; Hecht, 1974; Renaud and Schmidt, 2003; Schmidt et al., 2004b). For example, the variations in size and shape within certain species form geographical patterns that have been linked to salinity and temperature variations in the modern ocean (e.g. Hecht, 1974), and corroborated by laboratory culture experiments under varying salinity and temperature conditions (Hemleben et al., 1987; Bijma et al., 1990b). Furthermore, vertical habitat separation is reflected in the morphological stratification of the planktic foraminiferal ecosystem within the top hundreds of metres of the water column (Hemleben et al., 1989). Today, mixed layer species tend to have a rounded globular test, such as in the globigerinids, and are carnivorous and often carry symbionts, whilst the flattened discoidal, or conical forms, representing globorotaliid morphologies, generally live at or below the thermocline and are predominantly herbivorous (Brasier, 1986), though this pattern was not the same in the warm Paleogene where many keeled and planoconical forms inhabited the surface and subsurface waters, and most globular forms the deeper ocean (Olsson et al., 1999).

The close relationship between morphology and the environment has led to untested hypotheses of foraminiferal morphological evolution linked to changes in physical properties of surface waters (Malmgren and Kennett, 1981; Norris et al., 1993; Wei, 1994; Malmgren et al., 1996; Schneider and Kennett, 1996). Specifically, it has been suggested that foraminifera alter their shape and size, which determine their weight, their overall density, i.e. the ratio between calcite and protoplasm, and any frictional drag acting upon them, in direct response to changes in water density and viscosity to retain or modify their hydrodynamic behaviour accordingly. For example, the evolution from *Globoconella puncticulata* to *Globorotalia (Globoconella) inflata* is associated with an increase in inflation of the test, overall size, and peripheral roundness, which coincides with middle Pliocene cooling and an increase in stratification (Wei, 1994). These morphological changes have been suggested to have increased settling velocity for the lineage either to counteract the increase in water density and viscosity due to cooling in order to maintain the same water depth (Malmgren and Kennett, 1981; Wei, 1994), or to migrate to a deeper layer to exploit new niches made available by increased stratification (Schneider and Kennett, 1996).

In another classical study of morphological evolution, the *Globorotalia* (*Fohsella*) lineage, increases in size, axial compression and thickening of the peripheral keel were accompanied by an increase in $\delta^{18}O$ during the middle Miocene, which has been suggested to reflect a migration to a deeper habitat (Hodell and Vayavananda, 1993; Norris et al., 1993). These morphological changes would result in a decrease in buoyancy of the test, facilitating an adaptation to a deeper habitat. Alternatively, these morphological changes could be a result of growth in deeper waters through changes in growth rate, reproduction or trophic state associated with thermocline and chlorophyll maxima (Hodell and Vayavananda, 1993). Norris et al. (1993) also argue that most other morphological changes involving more radical changes in shell structure, such as the evolution of a compressed smooth-walled morphology and the acquisition of strongly angular peripheries, occurred in the near-surface waters and do not reflect a morphological change in response to a new habitat. Similar suggestions have been made for shifts in depth occupation of a number of species coincident with the earliest Cenomanian cooling trend which did not involve morphological changes (Ando et al., 2010). This leaves the important question of whether morphological evolution is solely, partially or indirectly related to the environment.

To assess the validity of the hypotheses linking planktic foraminiferal morphology to environment, we quantify the functional relationship between morphology and the surface water properties by looking at their settling velocity. We evaluate the prediction that the morphological change observed within evolutionary lineages and local morphological variations within species, as well as the depth-stratification of the foraminiferal ecosystem, reflect an adaptation to the surrounding water properties. Key morphologies within the planktic foraminifera were modelled under various idealised seawater conditions and the results compared with settling experiments of a number of foraminiferal species.

2. Materials and methods

To establish a framework within which to explore the effect of morphology on settling velocity, we carried out settling experiments of different species of planktic foraminifera representing key morphotypes. The limitation of settling experiments, however, is that the essential morphological variables of size, shape and density co-vary, meaning that their relative effects on settling cannot be isolated. The use of appropriately verified Computational Fluid Dynamics (CFD) simulations, in addition to simple settling experiments, allows manipulation of all variables independently, leading to a more systematic survey of the parameter space. This is particularly relevant in the settling regime of planktic foraminifera, as it falls outside that when Stokes' Law applies. Only empirical settling laws are available to assess the role of size, density and water properties. The validity of the simulations, here simplified to two dimensions, was verified against both empirical settling laws and against the settling experiments.

2.1. Experimental study

Specimens from the following nine foraminiferal species were picked from the >250 μm size fraction from sediment samples: near-spherical *Globigerinoides conglobatus* (n = 29) and *Orbulina universa* (n = 30); globular *Globigerinoides trilobus* (n = 26), *Globigerinoides sacculifer* (n = 28), and *Globigerinoides ruber* (n = 24); discoidal *Globorotalia menardii* (n = 30), and *Globorotalia tumida* (n = 30); lowly conical *Globorotalia hirsuta* (n = 29); and highly conical *Globorotalia truncatulinoides* (n = 29) (Fig. 1). The specimens were all from modern sediments in the Caribbean deposited significantly above the lysocline and did not show any signs of diagenetic overgrowth or dissolution. As the specimens either have large secondary apertures and small slit like apertures, there was little sediment in these specimens. To avoid breakdown of the calcite, we decided not to clean the specimens in an ultrasonic bath. The specimens were photographed in both face and side views under a Leica-mounted microscope, and maximum diameter measurements along three orthogonal axes were taken using ImageJ (version 1.44p; National Institutes of Health, USA) to calculate a basic total volume using formulae for cones (*G. truncatulinoides*), spheres (*O. universa*) and ellipsoids (all other species) (see Supplementary Information for raw measurements). The foraminifera were weighed in batches of 5 specimens of similar sizes from the same species, and the volume of calcite in each specimen was calculated assuming a calcite density of 2700 kg m^{-3} (Mann, 1986). The volume of the internal cavity was determined as the difference between the volume of calcite and the basic total volume, and a density was computed for each specimen, assuming the filling of the internal cavity with freshwater (density = 1000 kg m^{-3}).

Specimens were soaked in demineralised freshwater for two weeks to remove air bubbles. Specimens were then allowed to settle individually in a 140 mm diameter cylindrical tube filled with demineralised freshwater to a depth of 155 mm. This setup was sufficient for the foraminifera to reach terminal velocity, verified by measuring settling velocity over several depth intervals, with negligible wall effects (calculated following Di Felice, 1996). Descent was recorded using a high-speed camera (Vision Research Phantom v.9.1 at a sampling rate of 100pps with a 1440 × 720 pixel resolution and 3000 μs exposure) and terminal velocity was confirmed by calculation from 20 consecutive image frames from the lowest 30 mm.

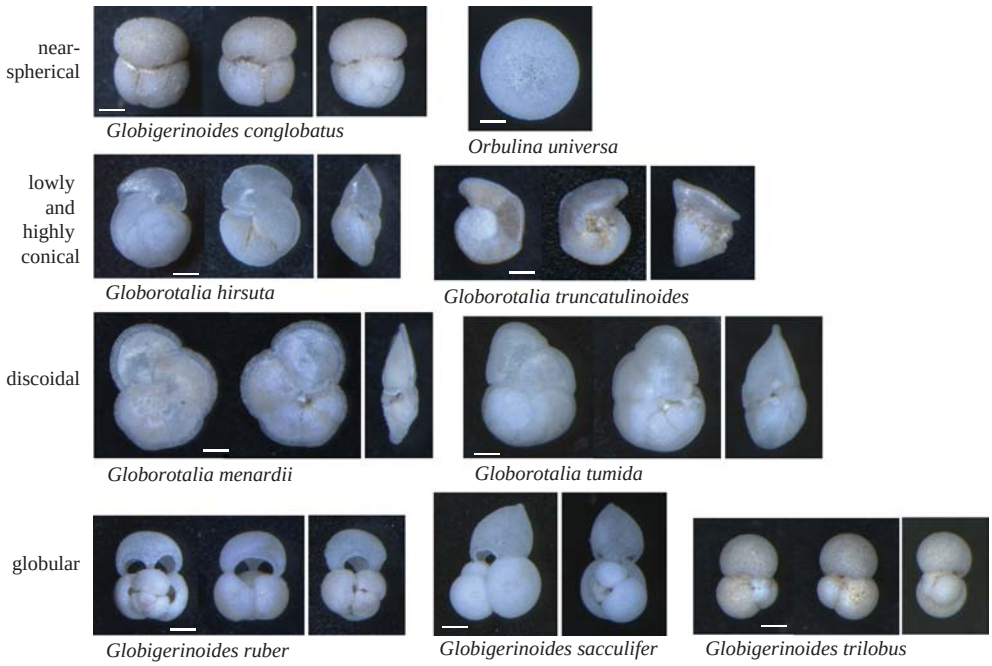

Fig. 1. Representative specimens for the foraminiferal species used in the settling experiments (scale bars 200 μm).

2.2. Modelling and simulation study

Two hundred and twenty simulations were run, varying extrinsic (fluid properties and object orientation) and intrinsic (object properties) parameters independently. Foraminiferal shape profiles were simplified to regular object shapes with quantifiable volumes: straight-edged cones and ellipsoids of varying aspect ratios (across-flow:along-flow length ratio), to generate shapes ranging in inflation from flattened discs to spheres (Fig. 2a). The flow around these idealised foraminiferal shapes (hereafter termed 'objects') was calculated in 2D using the finite element solver COMSOL version 3.5 (Fig. 2). The position and orientation of a symmetrical object were fixed, and the flow field was meshed relative to the object. Through repeated refinements of the mesh to ensure that results were independent of mesh resolution, it was determined that a coarse mesh with increasing element size further from the object was sufficient (Fig. 2b). The flow was nominally vertically upwards; we use the terms 'vertical' and 'horizontal' to represent the directions parallel to and perpendicular to the flow direction, respectively. The simulation field has open boundaries at top and bottom (with no compression or stress) to simulate flow through the domain; the boundary encompassing

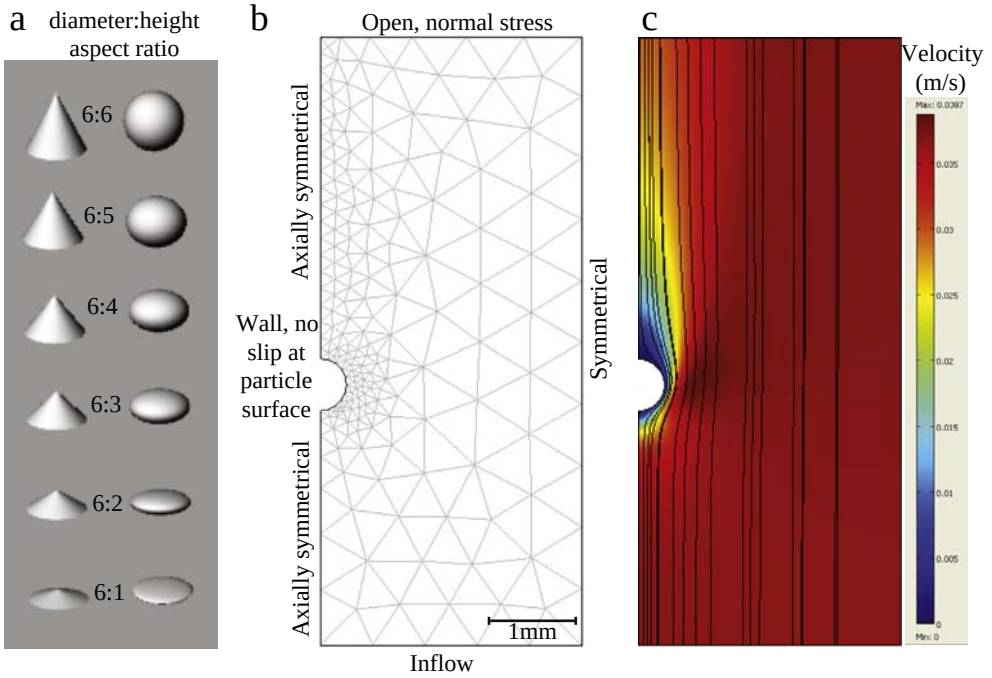

Fig. 2. COMSOL simulation setup. a) Representation of an axially symmetrical model in COMSOL, simulating the fall of a sphere, showing the fluid field mesh and boundary conditions; b) regular shapes simulated in the models; c) Solved model showing the local velocity variation (coloured) and streamline deformation (black lines).

the object reflected the symmetry of the simulation, and the remaining outer boundary was set to simulate an unconfined water column. At the object-fluid interface, the fluid velocity relative to the object was fixed as zero by locally assigning a no-slip boundary condition (Fig. 2b). The Navier–Stokes equation for settling particles, incorporating weight and buoyancy terms and the drag force calculated over the surface of the object, and continuity equations for increasing velocity were solved. Simulations were run from an initial condition of zero relative flow velocity to the point at which the terminal velocity was reached (defined as constant relative velocity).

In a first set of simulations, water properties were kept constant, representative of seawater of 35‰ salinity at a temperature of 20 °C (density $\rho_w = 1025$ kg m^{-3}; dynamic viscosity $\mu = 1.09$ mPa s), whilst object input parameters varied. The effect of changing size on settling velocity was investigated by running eleven simulations each of a sphere, a cone (aspect ratio 6:5) and a disc (aspect ratio 6:2) of varying diameters and keeping object density constant at $\rho = 1500$ kg m^{-3} based on the average density of a water-filled test determined by Berger and Piper (1972). Note that we use the term 'size' in relation to the longest linear dimension of an object. The simulation runs were also expressed in terms of weight.

In order to investigate the effect of shape on settling, six simulations each of ellipsoids and cones of varying aspect ratio but constant cross-section (diameter = 600 μm) and density ($\rho_o = 1500$ kg m^{-3}) were run. To explore the effect of size and shape changes, size and aspect ratio were simultaneously varied in a further six simulations each of ellipsoids and cones, with dimensions determined such that volume remained constant across all aspect ratios, and density was kept constant. Finally, to investigate the differences in calcification that might occur within foraminifera, object density was increased to 2700 kg m^{-3} (simulating an unrealistic end member object completely composed of calcite) in the six ellipsoids and cones of varying aspect ratio and constant cross-section (diameter = 600 μm).

In a second set of simulations, object parameters remained constant (diameter = 600 μm; $\rho_o = 1500$ kg m^{-3}; varying shapes) whilst the extrinsic parameters, water viscosity and density, were varied to match water properties at temperatures between 0 and 30 °C. The settling of cones (aspect ratio 6:5) was simulated with their base aligned horizontally either at the top or bottom, and ellipsoids of varying aspect ratios were simulated with their longest axis either horizontal or vertical. As both water viscosity and density vary when simulating changes in water temperature, the contribution of each to changes in settling velocity was tested by varying them independently for a sphere, cone (aspect ratio 6:5) and disc (aspect ratio 6:2) over the range of values representative of ocean conditions (ρ_w between 1022 and 1028 kg m^{-3} (Dorsey, 1968) and μ between 0.86 and 1.89 mPa s (Miyake and Koizumi, 1948)).

In addition to exploring the parameter space, two simulations were run varying extrinsic and intrinsic properties simultaneously, in the context of a case study of foraminiferal morphological evolution concurrent with changes in water properties. The change from a conical, keeled form *Globoconella conomiozea* in the Miocene, to a keel-less, peripherally rounded *G. inflata* in the late Pliocene is coincident with cooler recorded temperatures (Malmgren and Kennett, 1981; Schneider and Kennett, 1996). The morphology and size were taken from the study of Malmgren and Kennett (1981) to generate the shape profiles based on a side view of the specimens (Fig. 3); water properties were determined from temperatures inferred from the isotope signals from the study of Schneider and Kennett (1996) (*G. conomiozea* model: T = 12 °C, μ = 1.32 mPa s, $\rho_w = 1026$ kg m^{-3}; *G. inflata* model: T = 10 °C, μ = 1.41 mPa s, $\rho_w = 1027$ kg m^{-3}).

2.3. Mathematical validation and calculations

Because of the simplifications in object morphology in the simulations and the complexity of real foraminiferal tests, it is necessary to verify that the results of the simulations are realistic and can be compared with the foraminiferal settling experiments. This can be done by comparing simulation output terminal settling velocities with calculations using a standard empirically-derived correlation for spherical abiogenic particles:

$$Re = \left(2.33Ar^{0.018} - 1.53Ar^{-0.016}\right)^{13.3}$$

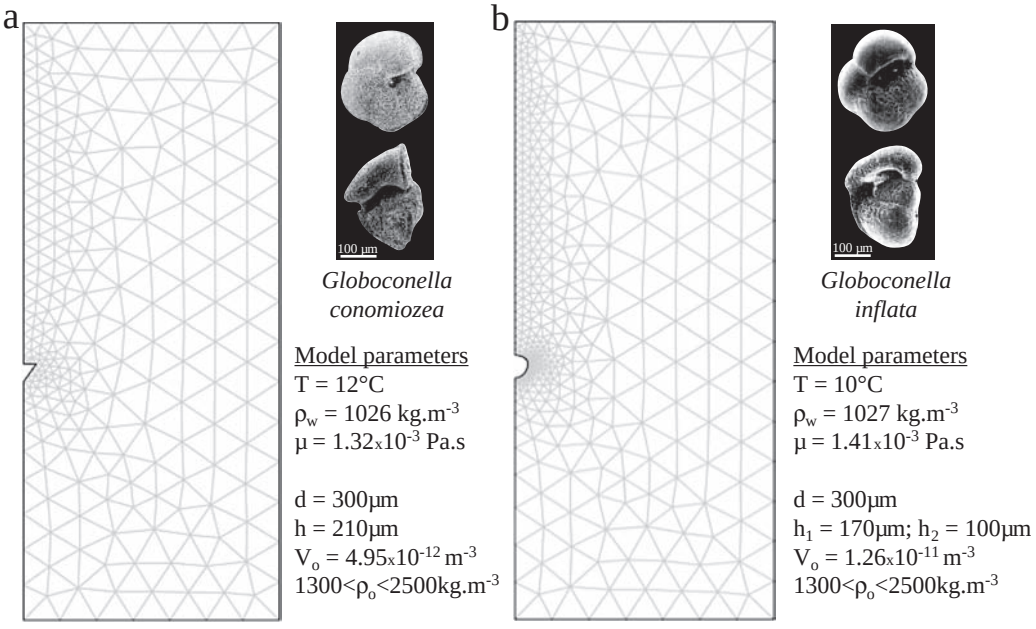

Fig. 3. *Globoconella conomiozea–inflata* lineage simulations. COMSOL simulation shape profiles of specimens in side view, representative specimens (umbilical face view, top; apertural side view, bottom), and model parameters for *Globoconella conomiozea* (a) and *G. inflata* (b). Representative specimens from Malmgren and Kennett (1981). T = temperature; ρ_w = water density; μ = viscosity; d = diameter; h = height; V_o = volume; ρ_o = object density.

(Coulson and Richardson, 1991). Here the particle Reynolds (ratio of inertial to viscous forces) and Archimedes (ratio of gravitational to viscous forces) numbers are defined respectively as

$$Re = D \cdot \rho_w \cdot v/\mu \quad \text{and} \quad Ar = D^3(\rho_o - \rho_w) \cdot \rho_w \cdot g/\mu^2$$

where D is the object (= foraminiferal) diameter, ρ_w and ρ_o are the water and object density respectively, v is the velocity, μ is the water dynamic viscosity and g is the gravitational acceleration. The applicability of this correlation for the experimental Reynolds number range was confirmed *a posteriori* as is standard practice. For the cases using regular simplified non-spherical shapes, a shape correction factor was applied using the methodology for non-spherical grains settling in a fluid presented by Coulson and Richardson (1991).

Using a combination of the mathematical equations and simulation settling velocity results, we calculated the morphological (size and density) changes required for an organism to maintain the same velocity under changing water conditions, such as a 5 °C change in water temperature, for objects of all shapes with a starting diameter of 600 μm and density of 1500 kg m^{-3}, and for the *G. conomiozea* and *G. inflata* simulations.

3. Results

3.1. Exploring the parameter space

The results of the foraminiferal settling experiments are consistent with expectations based on the empirical correlation for spherical abiogenic particles (Fig. 4a) for the range of Reynolds numbers characterising the settling of the foraminiferal tests in water (see Supplementary Information for raw settling data). Our results generally agree well with previous experiments; for example, Fok-Pun and Komar (1983) found settling velocities in *O. universa* between 0.02 and 0.06 m/s comparable to ours. Minor differences in settling velocities between studies can readily be explained by differences in the size fraction used for the experiment, for example the smaller sizes of *G. sacculifer* used in previous studies (Fok-Pun and Komar, 1983; Takahashi and Bé, 1984).

With water conditions equal across all settling experiments, three aspects of the foraminiferal test can govern settling velocity: size, shape and density. For equal size, more heavily calcified, and hence relatively denser species *G. conglobatus* (spherical), *G. truncatulinoides* (conical) and *G. tumida* (discoidal) have higher settling velocities than their less dense shape counterparts *O. universa*, *G. hirsuta* and *G. menardii* respectively (Fig. 4b). The trends for each species show

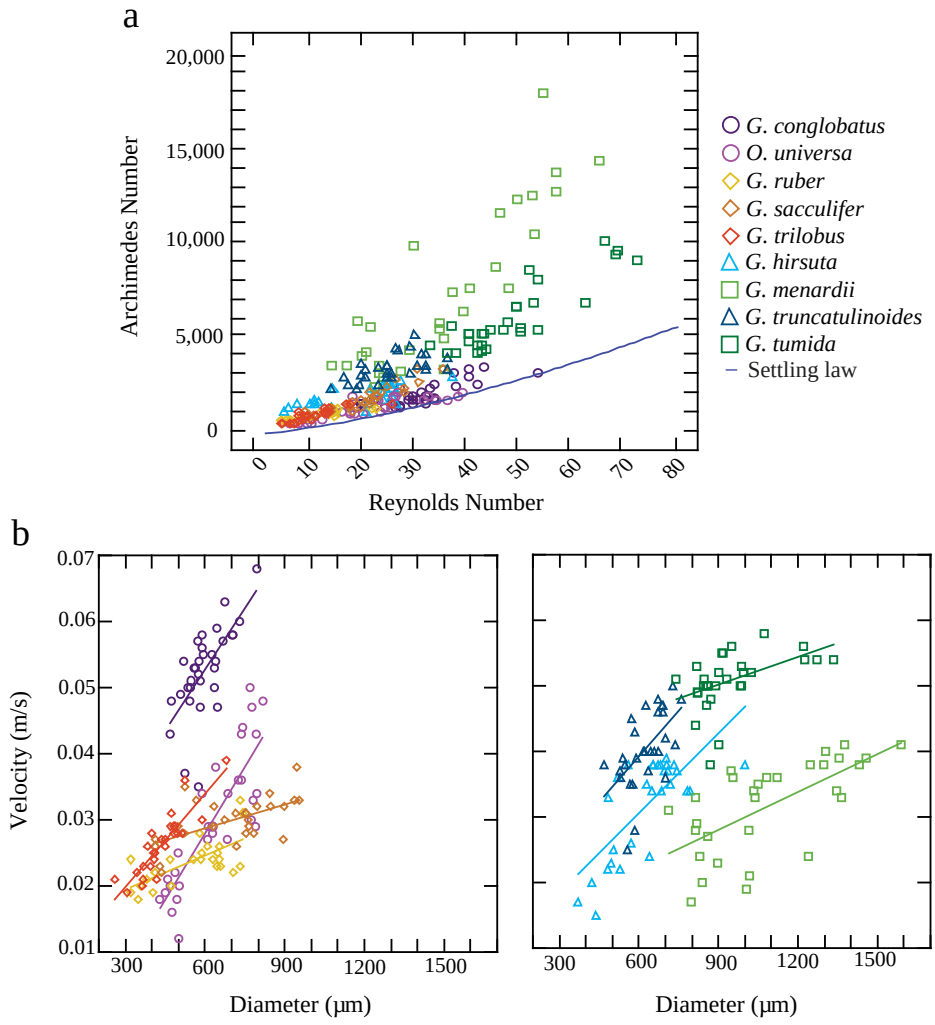

Fig. 4. Experimentally-determined settling velocities of foraminiferal tests. a) Reynolds vs Archimedes numbers measured for all species and predicted using the standard empirically-derived settling law, b) measured settling velocity of foraminiferal tests versus their diameter (legend as in a). Symbols: circles = species with high sphericity; triangles = species moderately to highly conical; squares = discoidal species; diamonds = globular/ellipsoidal species with high inflation.

that, for increasing size, spherical species have the greatest increase in settling velocity, followed by conical species, whilst flattened species have the lowest increase in settling velocity (Fig. 4b). Globular tests of intermediate inflation, exemplified by *G. ruber*, *G. sacculifer* and *G. trilobus*, have trends intermediate between those of flattened discoidal and spherical species. Because of the range in densities across species, however, absolute values of settling velocity between shapes cannot be compared directly, which is where the numerical simulations are informative.

Whilst numerical simulations allow us to address the relative effects of morphology more explicitly, a number of simplifications and constraints to the input variables are necessary for modelling, and their validity needs to be assessed. Firstly, the 2D COMSOL simulations produce terminal velocities that are in good agreement with velocities calculated from the empirical settling law calibrated for three-dimensional settling, as expected for shapes that have an axis of symmetry ($R^2 = 0.9787$). Secondly, the fixed orientation of the object in the simulations is consistent with previous experimental results for discoid object settling. These show that, at the range of Reynolds numbers for the numerical simulations (0.01–70), high aspect ratio shapes settle with their long axis perpendicular to their settling direction (Allen, 1982) and maintain this orientation during settling without rotation or precession (Allen, 2001), which was corroborated by our settling experiments. Results from the COMSOL simulations can therefore be readily compared with the settling experiments. The overall trends in velocity with shape and size from the settling experiments are corroborated by the modelled foraminiferal tests but also allow a more detailed investigation of factors influencing buoyancy and settling.

The simulation results show that settling velocity increases approximately linearly with size across all shapes when object density remains constant (Fig. 5a). For objects of constant density, volume and weight are proportional to the cube of size, corresponding to an approximately one-third power increase of settling velocity with volume or weight. As a consequence, increase in weight (or volume)

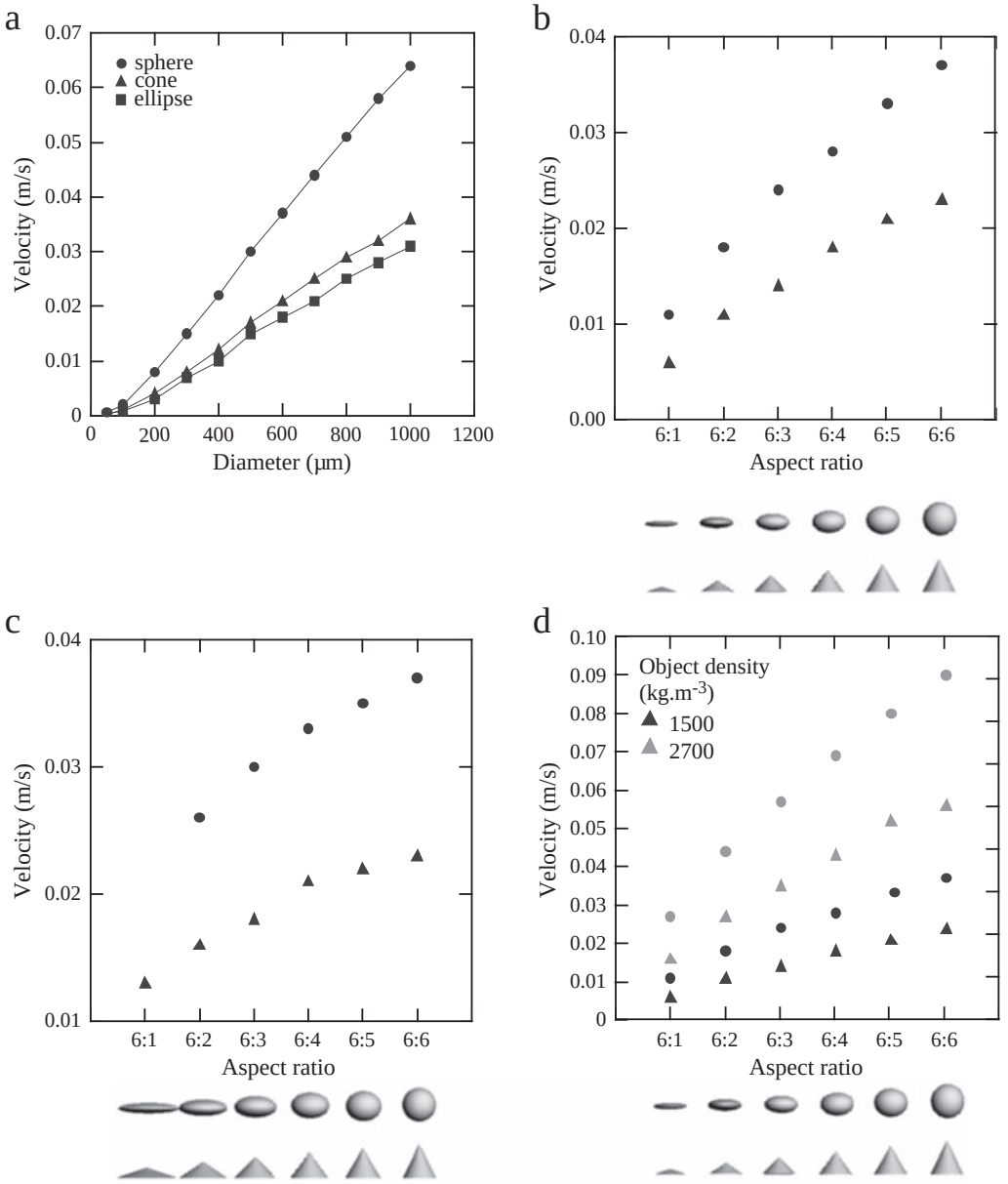

Fig. 5. Terminal velocity variation with size (a) and shape aspect ratio (b–d), from COMSOL simulations. (a) for a sphere (circles), cone (base diameter: height = 6:5; triangles) and ellipse (base: height diameters = 6:2; squares) with $\rho_o = 1500$ kg m^{-3}; (b) at constant cross-section and object density ($\rho_o = 1500$ kg m^{-3}); (c) at constant object density ($\rho = 1500$ kg m^{-3}) and varying cross-section such that volume is constant across all aspect ratios; and (d) at constant cross-section at $\rho = 1500$ kg m^{-3} and $\rho = 2700$ kg m^{-3}. Water properties characteristic of seawater at 20 °C.

produces a correspondingly smaller increase in settling velocity. Spheres have the highest settling velocity relative to cones and discs oriented with their circular cross-section perpendicular to the flow direction (i.e. horizontal orientation); the difference in settling velocity increases with increasing size, meaning that the larger the object, the greater the effect of shape on settling velocity.

The settling velocity of cones and ellipsoids increases with decreasing shape aspect ratio for a given cross-section (Fig. 5b), as a result of the increase in volume and hence weight at constant density. When volume or weight is held constant, increasing the aspect ratio results in an increase in cross-sectional area presented to the flow, and consequently lower settling velocity (Fig. 5c). Changing the object density had a greater effect on the velocity of objects with lower aspect ratios than those with high aspect ratios due to corresponding differences in volume (Fig. 5d).

All objects sink faster in warmer water (Fig. 6a). Increasing temperature from 0 to 30 °C only marginally amplifies any differences in settling velocity between shapes. Orientation has a greater effect on settling the greater the aspect ratio of the ellipsoid (Fig. 6b), due to the greater difference in cross-section presented to the flow between orientations. Over representative temperatures, the change in water viscosity with temperature is responsible for the velocity differences, whilst varying water density has no discernible effect (Fig. 6c).

3.2. Assessing palaeoenvironmental and evolutionary implications

Our simulation results show that, for 5 °C change in temperature, the required increase in test density to maintain the same settling velocity is in the range of 3–6% (50–100 kg m^{-3}; 5–10 μg), for an object of fixed size and shape. For an object maintaining the same density, the required increase in size to remain at the same settling velocity is in the range of 5–6% per 5 °C decrease in temperature, for all shapes. To assess if the above results can provide an explanation for evolutionary changes in morphology of planktic foraminifera, we applied them to one of the prime model cases — the *Globoconella conomiozea–inflata* lineage, with a change from a conical to a peripherally rounded form, coincident with a 2 °C cooling in surface waters (Malmgren and Kennett, 1981; Schneider and Kennett, 1996). The simulations of *G. conomiozea* and *G. inflata* show that even accounting for a change in temperature, the change in shape to *G. inflata* causes it to sink faster than *G. conomiozea* assuming the same size and density (Fig. 7). In order to obtain the same settling velocity for the two shapes under their respective temperature conditions, a decrease in test density of 20-30% from *G. conomiozea* to *G. inflata* would be required.

4. Discussion

While the relationship between settling behaviour and size, overall shape and surface ornamentation has been studied in phytoplankton (Conway and Trainor, 1972; Villareal, 1988; Padisak et al., 2003; Holland, 2010; Naselli-Flores and Barone, 2011) and abiogenic particles (McNown and Malaika, 1950; Komar and Reimers, 1978; Field et al., 1997), it has never been applied rigorously to planktic foraminifera. A link between form and flow regime in planktic foraminifera has been suggested based on the observation that different species favour different water-masses corresponding to their species-specific optimal growth conditions. The morphology of foraminifera has thus been related to their relative position in the water column, with modern globular forms in the more turbulent upper part of the water column whilst more conical and discoidal forms live deeper in calmer waters (Hemleben et al., 1989). Moreover, evolutionary adaptations to changing surface water properties, such as increased stratification due to cooling, have been linked to modifications of form such as test inflation and loss or acquisition of a keel (Malmgren and Kennett, 1981; Norris et al., 1993; Wei, 1994; Malmgren et al., 1996; Schneider and Kennett, 1996).

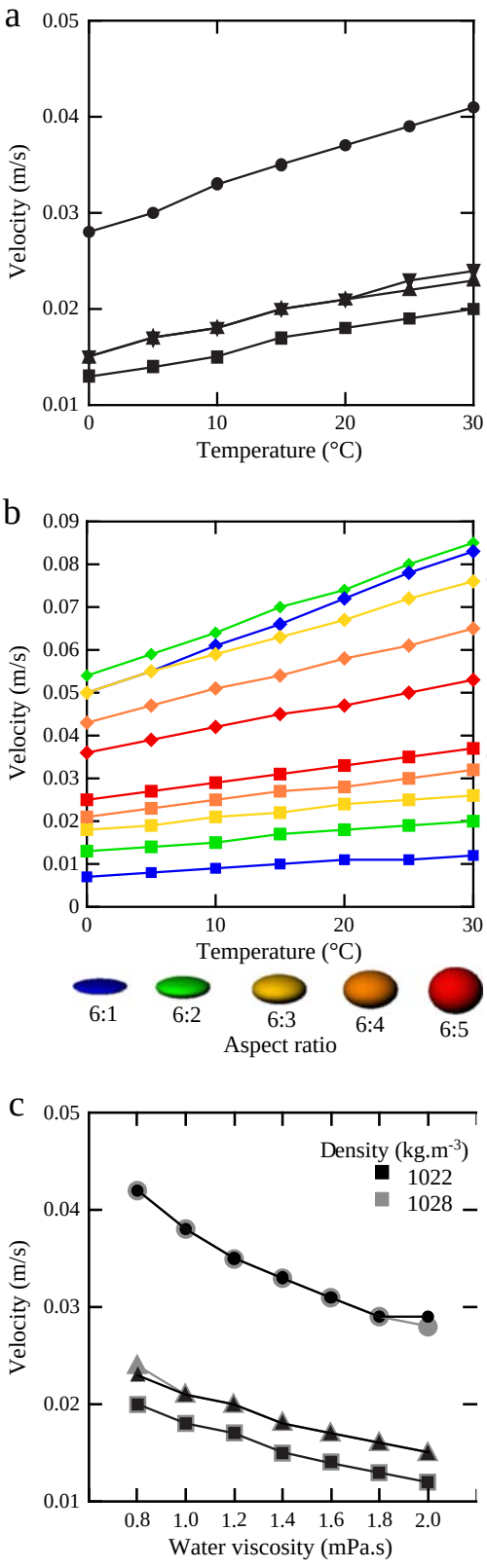

Fig. 6. Terminal velocity of objects against temperature in seawater (a–b) and under varying seawater viscosity at the highest (grey) and lowest (black) densities (c). For a sphere (circles), up- and down-pointing cones (up- and down-pointing triangles respectively) and ellipsoids in horizontal (squares) and vertical (diamonds) orientation. Base diameter of all shapes = 600 μm; cone aspect ratio 6:5; ellipsoid aspect ratio and 6:2 for a) and c), and colour-coded for b). From COMSOL simulations with ρ_o = 1500 kg m^{-3}.

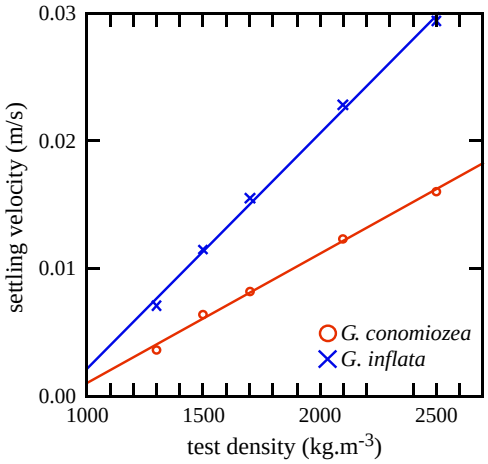

Fig. 7. Terminal velocity of the *Globoconella conomiozea–inflata* lineage simulations over a range of test densities. See Fig. 3 for other input variable values.

Test morphology is a compromise between function and a number of constructional and energetic constraints during development, and hydrodynamic function is thus only one potential influence. For example, test architecture may influence the communication of the cytoplasm between the innermost chambers and the environment (Brasier, 1982), or the position and extend of gas vacuoles especially in larger benthic foraminifers. As the test represents the form template for the cytoplasm, its surface area and morphology control the exposure of the cytoplasm to the environment for prey capture and nutrient exchange, and the exposure of symbionts to light (Hemleben et al., 1989).

Here, we focus on whether the test, which confers negative buoyancy to the foraminifer, can be exploited as a tool to minimise its impact on the life of the organism. It is important to note that therefore our modelling results are based on simplified shapes and do not represent the complex morphological variability in planktic foraminifera. The main omission is the lack of long acicular spines, found in many of the surface-dwelling globular forms. These spines generate additional drag which decreases the settling velocity (Takahashi and Bé, 1984), but extrusion of cytoplasm, both in form of a cover of the test and rhizopodia, during the day reduces the hydrodynamic advantage of the spines by decreasing the added surface area on which drag can act (Furbish and Arnold, 1997). Little is known about the temporally variable 3D-structure and density of these rhizopodia and therefore about their specific potential effects on hydrodynamics. Similarly, the effect of the density of the cytoplasm and the contribution of the living cell to buoyancy through active processes, as shown in phytoplankton (Smayda, 1970), is unknown; we used the average density of a water-filled test based on the fact that sinking experiments have shown that dead cytoplasm-filled tests have settling velocities similar to empty tests (Takahashi and Bé, 1984).

4.1. Links between depth ecology and shape

In general, high aspect ratio objects, such as a *G. menardii* shape, settle with their longest axis perpendicular to their vertical motion; so for objects of the same size and density, the more spherical the object, the faster the settling velocity. Hence, evolving a flatter shape will decrease the foraminifer settling velocity if it maintains the same size, or will permit an increase in size, which has been suggested to be ecologically and evolutionarily advantageous (Hecht, 1976; Schmidt et al., 2004a, 2004b), without detrimentally increasing its settling velocity. Similar velocities are indeed attained by the globular and discoidal forms in the settling experiments, but for much larger sizes in the latter group.

A consequence of a flatter shape at constant size is a decrease in volume. As the foraminiferal test houses the living cell, decreasing the test volume reduces the cytoplasm capacity of the organism, which determines the amount of gametes and reproductive success (Hemleben et al., 1989). Simulations of constant volume, however, show that despite the increase in size required to compensate for the change in shape, the benefit of flattening the shape to decrease velocity remains. Evolving a flatter shape would therefore enable the organisms to grow to larger sizes without decreasing their volume or increasing their settling velocity. In modern oceans, the discoidal forms *G. menardii* and *G. tumida* are by far the largest species (Schmidt et al., 2004b) and we suggest that their shape allows them to attain this large size. Having a large discoidal form increases the surface area, creating a larger food capture surface, useful in species dependent on encounter rates with their prey, or in the case of symbiont-bearing forms, increasing the area exposed to direct sunlight.

Based on these results, we would expect rounded morphologies to occupy deeper, cooler parts of the water column, where the lower temperature would help to reduce their settling velocity and maintain the organisms longer in the water column. The broad pattern of depth-stratification in the modern planktic foraminiferal ecosystem, however, is the opposite (Pearson et al., 2006). We suggest that turbulent mixing of the surface layers, which has been shown to counteract the negative buoyancy of phytoplankton shells (Huisman et al., 2002), allows globular foraminifera to live in the surface water and to exploit this habitat for their symbionts. This is aided by their faster reproductive cycle that reduces their required residence time in the ocean (Bijma et al., 1994), compared, for example, to the conical deep-dweller *G. truncatulinoides* (Hemleben et al., 1989). Under turbulent mixing, other factors underpinning morphology would dominate, such as heritage, exposure of the symbionts to light or oxygen diffusion into the cell, the latter being suggested for the shape changes in hantkeninids (Coxall et al., 2000). In such a setting, a non-equant organism would not be able to consistently maintain a preferred orientation, which would strongly influence settling velocity as well as only expose half the surface area to sunlight at any given time. In a stratified ocean at depth, however, suspension would not be aided by turbulent mixing and a preferred orientation could be maintained at the Reynolds numbers associated with settling motion. Developing a shape which hinders settling would therefore become more advantageous. Intriguingly, a hydrodynamically expected order in the depth stratification of foraminifera morphologies, reversed to today, was present in the Paleogene ocean, an environment with more homogenous upper water temperatures (Pearson et al., 2001) and less stratification (Schmidt et al., 2004a), possibly reflecting a weaker turbulence profile of the upper water column.

Species carrying symbionts have life cycles in the upper layers of the water column on the order of 2–4 weeks (Bijma et al., 1990a), whilst *G. truncatulinoides* appears to reproduce annually (Spear et al., 2011), after having migrated to the surface from deeper waters (Schiebel and Hemleben, 2005). The settling velocities measured here are on the order of several thousand metres per day, which would mean settling out of the mixed layer in a matter of hours. This implies that a number of other mechanisms, as those invoked in the phytoplankton, must keep foraminifera in suspension. Furthermore, planktic foraminifera are thought to migrate through the water column as they grow (Emiliani, 1971; Hemleben et al., 1989). It would be interesting for future ontogenetic studies to consider how changes in shape and calcification during ontogeny could relate either to the differences in habitat undergone with depth migration, or to mechanisms to resist such a migration. However, the lack of knowledge of the role of the living cell, such as the amount of vacuoles it can have, the amount of lipids these can host, and even the precise density of the living organisms, combined with the lack of a quantified understanding of the impact of turbulence in suspension, which is likely to be greater the smaller the foraminifer, currently prevents us from precise calculations.

4.2. Shape changes as a tool for evolutionary adaptation

Morphological evolution in some foraminiferal lineages has been directly related to changes in water properties (Norris et al., 1993; Malmgren et al., 1996), including porosity and aperture size (Frerichs et al., 1972; Malmgren et al., 1996). A change in environmental conditions might necessitate morphological evolution to either maintain the same depth (Malmgren and Kennett, 1981; Wei, 1994), or to alter their settling velocity to migrate to a new habitat (Schneider and Kennett, 1996), though not all shifts in depth involve morphological changes (Ando et al., 2010).

In addition to size and shape, density can be manipulated to alter settling velocity by changing calcification. More heavily calcified foraminiferal species settled faster in the settling experiments for similar shape and size. Decreasing density, for example by losing a keel or increasing pore area, would permit the organisms to grow to a larger size or evolve a more spherical shape whilst maintaining a similar settling velocity, or decreasing settling velocity whilst maintaining shape and size. For example, the spherical *O. universa* is larger in tropical areas, where decreased water viscosity would compound the increased settling velocity due to larger size. A decrease in wall thickness and doubling of porosity (Bé et al., 1973) is an efficient way for the species to maintain its buoyancy whilst allowing this size increase. Our results also show that a larger change in density would be required in foraminifera with a flatter morphology compared to round species to achieve the same modification in settling velocity. It has frequently been suggested that species with a non-globular morphology are less able to morphologically evolve into new shapes. It is possible that this, combined with a necessity for larger changes in density, contributes to making these species more prone to extinction (Arnold et al., 1995).

In our model linage, the change from a conical, keeled *G. conomiozea* to the keel-less, peripherally rounded *G. inflata* has been proposed as a means to maintain buoyancy in a cooling ocean (Malmgren and Kennett, 1981; Wei, 1994) or to migrate to a deeper, cooler layer to exploit new niches made available by increased stratification (Schneider and Kennett, 1996). Our temperature simulations predict that the observed increase in sphericity would lead to a much greater settling velocity. In order to obtain the same settling velocity for the two shapes under their respective temperature conditions, a decrease in density of 20–30% would be required from *G. conomiozea* to *G. inflata*. The loss of the keel of *G. conomiozea* would decrease the density but is likely offset by wall thickening and encrustation in *G. inflata* (Malmgren and Kennett, 1981; Hemleben et al., 1989). The additional increase in overall test size in *G. inflata* would also serve to increase the settling velocity. We therefore disprove the hypothesis that the change in morphology could have been effective as a means to maintain buoyancy. In contrast, our data corroborates the hypothesis of a migration of the lineage to a deeper part of the water column as a result of the density modulations and agrees with suggestions by Hodell and Vayavananda (1993) that keel thickening and increased size in *Globorotalia* (*Fohsella*) are morphological adaptations to the deeper habitat. This result also implies that a modification of test density, either abiotically via changing amounts of calcite or biotically via changes in density of the protoplasm, may be the easier or preferred way of foraminifers to alter settling velocity while still alive.

Across all shapes, for every 5 °C change in temperature, we estimate a required change in density of 3–6% or 5–6% in size to maintain the same settling velocity. These changes are small compared to within-species natural variability which can be exploited by natural selection (e.g. 25–50% increase in density due to secondary encrustation in *G. menardii* and *G. tumida* (Schweitzer and Lohmann, 1991)) and size ranges of several hundreds of micron within a species (Schmidt et al., 2004b). The morphological parameters by which species determine settling velocity, if at all, are therefore more likely based on other constraints on size, shape and calcification.

5. Conclusions

The range of evolutionary options open to plankton to modulate settling velocity under varying oceanic conditions is a result of trade-offs between combinations of changes in size, shape and density. Evolving a flatter shape allows to decrease settling velocity if maintaining the same maximum diameter. Alternatively, it allows growth to larger sizes without losing internal volume or sinking faster through the water column. Decreasing density, i.e. the relative ratio between calcite and cavity volumes, enables an organism to grow larger, to become rounder whilst maintaining settling velocity, or to sink more slowly whilst maintaining size and shape. Evolving towards flatter, less round shapes would become more advantageous in deeper, calmer waters. In contrast under turbulent mixing in surface waters, other factors underpinning morphology, such as metabolic and constructional costs, likely play a more important role than function in dictating test morphology in planktic foraminifera. Changes in physical properties of the habitat arising from environmental changes can easily be accommodated by the natural within-population variability, as can be found in the modern ocean with the latitudinal changes in wall thickness and porosity of *O. universa* (Bé et al., 1973). A larger change in density is required in species with a flatter morphology compared to a rounder one, and this might be a contributing factors to the fact that flatter species are more prone to extinction (Arnold et al., 1995).

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Appendix A. Supplementary data

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